

POSTCRANIAL ELEMENTS OF THE EXTINCT CONDOR

BREAGYPS CLARKI (MILLER)¹

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ABSTRACT: When the genus *Breagyps* was established, only the skull and tarsometatarsus were described. Other skeletal elements in the Rancho La Brea collections of the Natural History Museum of Los Angeles County are now assigned to *Breagyps* and are described in detail in comparison with bones of the two existing condor genera, *Vultur* and *Gymnogyps*. Contrasts with the smaller vultures are also noted. Resemblance is closest to *Vultur*, but distinctive generic characters are clear throughout.

INTRODUCTION

Breagyps clarki was first described (Miller, 1910:11) under the genus "*Sarcorhamphus*" (= *Vultur*) in comparison with *Vultur gryphus*. The type, and only known element at that time, was a tarsometatarsus in the collections of the University of California, Museum of Paleontology, from the Pleistocene of Rancho La Brea (UCMP 12588). With the later assignment to this species of skull material in the Rancho La Brea collections at the Natural History Museum of Los Angeles County (LACM), the genus *Breagyps* was erected (Miller and Howard, 1938:171). At this time the tarsometatarsus was restudied and generic characters of this element, as well as the skull, were delineated.

A complete review of all condor bones in the LACM collections from Rancho La Brea has resulted in segregating eleven other limb and girdle elements as well as several vertebrae, all of which are distinguishable from specimens of the better represented California Condor, *Gymnogyps*. The elements form a homogeneous group of approximately 150 bones whose characters are compatible with those of the tarsometatarsus and skull of *Breagyps clarki*. Therefore, I have no hesitation in assigning them to this genus and species.

During study of these elements of *Breagyps*, all present-day cathartid genera were compared. Each of these was found to share one or more separate characters with one or another genus of the family. But differences also appear in each element, and the combination of characters is distinctive for each genus. This is true, as well, of *Breagyps*.

In order to simplify the description of the elements now to be described,

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the detailed study of the fossil bones is confined to comparison with modern skeletal material of *Vultur gryphus* and *Gymnogyps californianus*. Comments concerning comparisons with the smaller vultures are included in the Discussion section.

MATERIAL AVAILABLE

All material is in the LACM collections except two modern skeletons of *Vultur gryphus*, which were loaned by the University of California at Los Angeles, Department of Zoology.

FOSSIL SPECIMENS

Breagyps clarki

(LACM catalog numbers)

STERNUM: six incomplete, B1517, B3071, B3372, B3783, B4554, B5669.

FURCULA: one symphysis, B6035; four clavicles, B2224, B2601, B8114, B8315.

CORACOID: nineteen nearly complete, B1499, B1638, B1739, B2311, B2644, B3242, B3424, B3821, B6188, B6320, B7067, B7124, B7479, B7699, B7743, B7847, B7914, B8039, B8376.

SCAPULA: one complete, B4450; ten articular ends, B1657, B1670, B1671, B1676, B2259, B3420, B3482, B4418, B6020, B6332.

HUMERUS: four nearly complete, B4847 + B5329, B7730, B7737 + B7739, B8002; five proximal ends, B1583, B2083, B2156, B4954, B5917; three distal ends, B2034, B5956, B7247.

ULNA: nine proximal ends, B1859, B1910, B3838, B4221, B4630, B6912, B6925, B7248, B8310; five distal ends, B3453, B5891, B6914, B7503, B7715.

RADIUS: one proximal end, B6782; one distal end, B7661.

CARPOMETACARPUS: fourteen nearly complete, B1075, B1755, B2168, B2632, B3154, B3271, B3625, B4160, B4375, B5331, B6395, B6712, B7608, J9402.

PELVIS: one nearly complete, B1082 + B1092; five incomplete, B1635, B3346, B6859, B6865, B7895.

FEMUR: eight nearly complete, B1404, B3358, B4989, B5580, B5693, B6259, B7493, B7803; two incomplete proximally, B2599, B6910; two proximal ends, B2257, B6372; six distal ends, B1437, B1574, B3388, B5950, B6620, B7460.

TIBIOTARSUS: three nearly complete, B4039, B5878, B6413 + B6414; one incomplete proximally, J9629; four proximal ends, B2115, B2314, B3361, B6404; nine distal ends, B1074, B1593, B2116, B3383, B5156, B6477, B7085, B7244, B8313.

CERVICAL VERTEBRAE: B3841, B3945, G9423, G9346 (atlas).

Additional specimens of these elements were used in the composite mount of *Breagyps clarki* now on exhibit at LACM: sternum B1428; furcula B8308 + B8309; coracoid B1495, B3837; scapula B4862, B7558; humerus B3246; ulna, proximal end B4458, B3353, distal end B592, B1665; carpometacarpus B2181, B2667; pelvis B4912 + B5165; femur B3379, B3576; tibiotarsus B7026, B7746. For an illustration of this mount, see Howard (1962: 29, fig. 12).

MODERN SPECIMENS

Gymnogyps californianus: 1 complete skeleton, 2 with wing bones only, 7 body skeletons.

Vultur gryphus: 2 complete skeletons.

Sarcoramphus papa: 1 complete, 1 body skeleton.

Coragyps atratus: 3 complete, 1 body skeleton.

Cathartes aura: 1 complete, 1 body skeleton.

As a further check on comparisons between genera of the family Cathartidae, Fisher's (1946) monograph on the comparative anatomy of this family was consulted.

DESCRIPTION OF ELEMENTS ASSIGNED TO *Breagyps clarki*

Sternum (Figure 1): Relatively broad across shield but short through costal row (see Table 1); anterior contour (viewed dorsally) broad and straight with lateral borders of dorsal lip of coracoidal sulcus protruding and tending to be square in outline; dorsal surface of shield deeply depressed close to anterior border on either side of a narrow central ridge; carina deep and ascending abruptly at level of last costal process; anterior border of carina depressed between central and lateral ridges; small, roughly triangular depression on ventral labial prominences, rimmed at lateral edge by rounded ridge and medially by external intermuscular line; ventral manubrial spine facing anteroventrally with long ridge rising to dorsal edge.

Vultur is generally similar in proportions and in anterior contour dorsally, but the carina is slightly lower and point of ascent farther posterior; the dorsal depression of the shield is less; the ventral labial prominences are

TABLE 1
Measurements of Sternum
(in millimeters)

	<i>Breagyps clarki</i> (3 bones)			<i>Gymnogyps californianus</i> (4 bones)			<i>Vultur gryphus</i> (2 bones)	
	max.	mean	min.	max.	mean	min.	max.	min.
Length from dorsal lip through last costal process	76.2	73.7	72.0	81.0	77.7	75.7	84.6	78.9
Length costal row	46.9	44.9	43.5	50.7	49.0	47.4	49.4	46.0
Breadth of shield back of second costal process	73.8	72.7	71.0	72.3	69.0	66.5	80.4	74.3
Breadth across ventral labial prominences	66.2	64.5	62.2	61.0	60.6	60.0	67.4	61.6
Ratio (in %) breadth shield to length from dorsal lip through last costal process	101.0	98.6	96.2	94.2	88.6	85.5	95.0	94.2
Ratio (in %) length costal row to breadth of shield	64.0	61.8	59.0	74.7	71.2	66.8	62.0	61.5

rounded ventrally, lacking the triangular depression found in *Breagyps*. In *Gymnogyps* the shield is relatively narrower, and anteriorly the contour is more curved; the carina is lower, with point of ascent well posterior to last costal process; the anterior surface of the carina slopes away laterally from the central ridge, with no lateral ridges; the depression on the ventral labial prominences is similar to that in *Breagyps* but somewhat longer. The ventral manubrial spine is more prominent in both *Vultur* and *Gymnogyps*, with a shorter ridge above.

Furcula (Figure 2D): Condorlike in the broad, gradual dorsal curvature of the clavicles; the arch is narrower and more abrupt in the other three cathartid genera. Externally, deep pneumatic fossa undercutting dorsal rim of clavicle as in *Gymnogyps*, but of less extent ventrally, stopping short of ventral border as in *Vultur*, but dorsal rim less undercut in *Vultur*. Area anterior to pointed scapular tip (externally) with shelflike expansion ventrally, narrowed abruptly dorsally with a large foramen between; unlike both *Gymnogyps* and *Vultur* in this character. (Although there is more expansion in *Gymnogyps* than in *Vultur*, it is gradual with multiple, small foramina, and the dorsal area is less narrowed.)

TABLE 2
Measurements of Coracoid
(in millimeters)

	<i>Breagyps clarki</i> (10 bones)			<i>Gymnogyps californianus</i> (8 bones)			<i>Vultur gryphus</i> (2 bones)	
	max.	mean	min.	max.	mean	min.	max.	min.
Length to sternal end mediad of angle	102.0	98.7	95.4	98.9	96.4	92.9	104.0	96.9
Breadth across triosseal canal	21.8	21.2	20.3	23.1	21.6	20.4	23.2	20.7
Breadth furcular facet	26.0	24.3	22.7	26.2	24.7	22.9	31.6	27.5
Height furcular facet	15.2	13.5	12.6	12.8	11.9	11.3	15.2	14.5
Ratio (in %) breadth triosseal canal to length of coracoid	22.2	21.3	21.0	23.5	22.4	21.0	22.2	21.4
Ratio (in %) breadth furcular facet to length of coracoid	26.6	24.6	23.7	26.5	25.6	23.5	30.3	28.2
Ratio (in %) height to breadth of furcular facet	58.6	55.6	51.6	51.5	48.2	45.5	52.7	48.1

Coracoid (Figure 2A,C): Head more prominently developed posteriorly than anteriorly, with diagonal groove through furcular facet emphasizing this unevenness; ligamental attachment on postero-external part of head short and deep, further increasing prominence of head posteriorly; neck well depressed; furcular facet high relative to breadth (see Table 2); anterior half of furcular facet narrowed and brachial tuberosity projecting anteriorly over deep fossa; fossa bordered externally by flange of bone, internally by sharply ridged edge of triosseal canal; lower margin of furcular facet concave near posterior edge, slightly overhanging triosseal canal.

The head is more evenly proportioned in the other two condors and the ligamental attachment on the postero-external part of the head is less prominent, the neck less depressed. In *Gymnogyps* there is a faint diagonal depression in the furcular facet, none in *Vultur*. The fossa below the brachial tuberosity is less developed in *Gymnogyps*, with the internal border of the triosseal canal rounded; the fossa is most markedly developed in *Vultur*, where the external flange of bone projects beyond the acutely bordered edge of the triosseal canal. The lower margin of the furcular facet is straight in both *Vultur* and *Gymnogyps*, with no overhang in *Gymnogyps*, a slight overhang in *Vultur*.

Scapula (Figure 2B): Acromion short and flaring abruptly from shaft, then markedly deflected mediad; dorsal contour of acromion (viewed externally) gradually rounded and, in proximal view, anterior projection of acromion broadly rounded; coracoidal articulation low; dorsal area between acromion and glenoid facet broadly depressed. See Table 3 for measurements.

The acromion rises gradually in *Gymnogyps* and is only faintly deflected; the dorsal contour is rounded but, as viewed proximally, the anterior projection is pointed; the coracoidal articulation is convex. In *Vultur* the acromion arises abruptly from the shaft but is less flared and is not deflected mediad;

TABLE 3
Measurements of Scapula
(in millimeters)

	<i>Breagyps clarki</i> (7 bones)			<i>Gymnogyps californianus</i> (8 bones)			<i>Vultur gryphus</i> (2 bones)	
	max.	mean	min.	max.	mean	min.	max.	min.
Breadth through acromion and glenoid facet	32.2	30.3	28.7	30.5	28.8	27.6	29.8	26.8
Length of acromion	23.3	22.1	21.5	22.0	21.0	20.2	24.3	24.0
Ratio (in %) length of acromion to breadth of scapula	75.4	71.8	68.5	75.0	72.9	68.5	89.5	81.2

in external view the dorsal contour is more angular and the anterior projection more prominently and acutely produced; the coracoidal articulation is low. In both *Gymnogyps* and *Vultur*, the space between the acromion and glenoid facet dorsally is narrower and less depressed than in *Breagyps*.

Humerus (Figures 3 and 5B): Bicipital crest broadly rounded; deltoid crest with even curvature, depressed medially (on anconal side) with raised, evenly contoured border; pectoral attachment widening gradually from a point proximal to level of distal border of bicipital crest; distal tip of pectoral attachment near edge of shaft; slightly pneumatic, shallow depression below head, palmad. Distally, deep pneumatic depression between internal condyle and attachment of anterior ligament and between external condyle and base of ectepicondylar prominence; ectepicondylar prominence broad and anconal border slightly concave.

Vultur resembles *Breagyps* in the shape of the bicipital crest, gradual widening and lateral termination of the pectoral attachment, and the shallow depression below the head; the bicipital crest is not as prominently protruded, however, and the pectoral attachment is narrower and does not extend as far proximally. *Gymnogyps* is distinct in all these features of the proximal end—the bicipital crest is less round especially at the distal terminus, the pectoral attachment broadens abruptly and its distal tip is mediad to the edge of the shaft, and the depression below the head is deeper and more pneumatic. In neither *Vultur* nor *Gymnogyps* is the deltoid crest as medially depressed, and the rim is not raised in an evenly contoured border. Distally, the degree of pneumaticity in *Gymnogyps* closely parallels the condition in *Breagyps* and the ectepicondylar prominence is close in size but is less curved. This prominence is longer, narrower and more curved in *Vultur*.

Length is probably a significant character of this element in *Breagyps clarki*. Four complete bones average 10 mm shorter than the mean of four humeri of *G. californianus*, and the minimum is 13 mm less than the *G. californianus* minimum (see Table 4). In all other limb elements *B. clarki* exceeds *G. californianus* in length.

Ulna (Figure 4A,B): Brachial impression well depressed, with large pneumatic foramina, and area between impression and internal cotyla swollen; distally, external condyle short and broad and closely appressed to shaft. As there are no complete ulnae of *Breagyps*, the number of anconal papillae for attachment of the secondaries, and the total length of the element can only be estimated. See Table 5 for estimated length; the number of papillae is at least 17 and possibly 19.

In both *Vultur* and *Gymnogyps* the area proximal to the brachial impression merges more gradually towards the cotyla; distally the external condyle is narrower and in *Gymnogyps* it is of greater proximo-distal extent. The number of anconal papillae in *Vultur* is 17-19, *Gymnogyps* has fewer (15-16). The number is still less in the smaller vultures. The fossil appears to exceed both modern condors in ulnar length.

TABLE 4
Measurements of Humerus
(in millimeters)

	<i>Breagyps clarki</i> (6 bones) ^a			<i>Gymnogyps californianus</i> (4 bones)			<i>Vultur gryphus</i> (2 bones)	
	max.	mean	min.	max.	mean	min.	max.	min.
Greatest length	267.0	261.2	256.0	275.0	271.7	262.0 ^b	280.0	272.2
Greatest breadth proximally through bicipital crest	60.1	59.1	58.6	58.3	55.8	54.0	62.1	57.9
Greatest breadth distal end	49.2	48.1	46.7	47.8	47.1	46.2	52.3	49.5
Length deltoid crest to distal tip pectoral attachment	116.5	111.9	106.2	118.7	116.0	114.2	122.2	114.5
Ratio (in %) proximal breadth to length		22.0		20.6	20.0	19.6	22.0	21.3
Ratio (in %) breadth distal end to length	18.8	18.4	17.9	17.5	17.3	17.1	18.7	18.2
Ratio (in %) length deltoid crest to length humerus	43.5	42.7	41.6	42.7	42.5	42.3	43.6	42.0

^aMeasurement of length could be made on only 4 bones and ratio of proximal breadth to length on only one.

^bFisher's (1947:229) measurements on 11 humeri: 274-262, mean 267 mm.

Radius (Figure 5A,C): With only one proximal and one distal end of this element for *Breagyps*, any description is necessarily tentative. Based on variability as observed in the other cathartid genera, the following characters are probably valid: bicipital tuberosity clearly bordered and set well below (21.9 mm) the proximal articular facet; capital tuberosity prominent; distal end flaring abruptly from shaft and ulnar depression broad and deep.

In *Gymnogyps* the bicipital tuberosity is set higher (17-19 mm below facet), the capital tuberosity is less prominent, the distal end more gradually flared and the ulnar depression very shallow. *Vultur* is more like *Breagyps* proximally; distally the ulnar depression is also somewhat as in *Breagyps*, but the distal flare is more gradual.

Carpometacarpus (Figure 4C): Process of metacarpal 1 heavy and slightly upturned; proximal and distal symphyses short (see Table 6); proximal symphysis well depressed; tuberosity of metacarpal 3 (proximally) a prominent

TABLE 5
Measurements of Ulna
(in millimeters)

	<i>Breagyps clarkia</i> ^a			<i>Gymnogyps californianus</i> (3 bones)			<i>Vultur gryphus</i> (2 bones)	
	max.	mean	min.	max.	mean	min.	max.	min.
Greatest length	365		341	320	315	312 ^b	354.0	330.0
Length to proximal cotylae	341		321	303.3	300.2	297.0	337.0	313.0
Breadth across proximal cotylae	31.7	30.7	30.0	33.0	31.5	30.6	32.6	30.5
Depth proximal end (externally)	26.8	26.3	25.9	25.5	24.9	24.4	28.5	26.7
Breadth distal end		25.5		22.7	22.5	22.2	25.0	22.3
Depth distal end externally		21.6		23.6	22.9	22.6	25.2	22.8

^aNo complete ulnae; measurements of length estimated; proximal breadth taken on 5 bones, distal breadth on only one.

^bFisher's (1947:229) measurements on 8 bones: 320-305, mean 313 mm.

tubercle; viewed posteriorly, internal trochlear crest narrowing abruptly distally on internal edge and joining shaft abruptly with ridge below; tuberosity of metacarpal 2 (distally) short but prominent, forming the median border of an anterior depressed area which is also heavily rimmed distally.

The process of metacarpal 1 is more anteriorly projected in the other condors but lower in proximo-distal dimension. Also, in the existing genera, the proximal symphysis is less depressed and the tuberosity of metacarpal 3 is less prominent. The length of the proximal symphysis is similar in *Vultur*, longer in *Gymnogyps*; distally the reverse is true, *Vultur* having a very long, flat symphysis. In both *Vultur* and *Gymnogyps* the internal trochlear crest is evenly rounded and lacks the abrupt narrowing as viewed posteriorly. Distally the tuberosity of metacarpal 2 is longer, less prominent and more ridgelike in *Vultur* and *Gymnogyps*. In *Vultur*, however, the anterior face of metacarpal 2 is depressed as in *Breagyps* and is heavily rimmed distally; *Gymnogyps* lacks the anterior depression but is more depressed internal to the tuberosity. See Table 6 for measurements.

Pelvis (Figures 6,7): With only one *Breagyps* pelvis even fairly complete, the characters of this element are indecisive. The following appear to be distinctive. Allied with condors in distinction to other cathartids in having three thoracic vertebrae attached to the synsacrum. Iliia not extending to anterior end of synsacrum; ilio-ischiatic surface deep with borders of ilia and ischia nearly parallel for a distance of about 30 mm posterior to acetabulum; iliac

TABLE 6
Measurements of Carpometacarpus
(in millimeters)

	<i>Breagyps clarki</i> (11 bones)			<i>Gymnogyps californianus</i> (2 bones)		<i>Vultur gryphus</i> (2 bones)	
	max.	mean	min.	max.	min.	max.	min.
Length from external trochlea to distal end metacarpal 2	145.9	141.1	134.5	136.1	135.8 ^a	143.5	136.7
Length proximal symphysis (to pisiform process)	30.8	28.6	26.9	31.3	31.1	28.0	26.3
Height process metacarpal 1	15.9	14.4	13.5	13.4	13.0	12.7	12.4
Length distal symphysis (to distal tip metacarpal 3)	17.7	15.5	13.3	15.7	15.6	21.3	20.7
Ratio (in %) length proximal symphysis to overall length	21.9	20.1	18.8	23.0	22.8	19.5	19.3
Ratio (in %) height process metacarpal 1 to overall length	11.2	10.1	9.6	9.8	9.5	9.1	8.8
Ratio (in %) length distal symphysis to overall length	12.3	11.1	9.2	11.6	11.4	15.1	14.8

^aFisher's (1947:230) measurements on three bones: 133-131 mm.

crest jutting out above acetabulum and ilio-ischiatic fenestra, the postacetabular ilia receding below the crest in the fenestral area; dorsal surface of shield moderately convex in midline, slightly depressed laterally and perforated with evenly spaced, fairly large pneumatic openings posteriorly, smaller openings farther forward; in ventral view, widest portion of synsacral caudal area posterior to acetabulum and flush with ventral surface of posterior ilia. See Table 7 for measurements.

Vultur resembles *Breagyps* in the extent of the anterior ilia; in *Gymnogyps*, the ilia extend only to the anterior border of the second synsacral thoracic vertebra. In both *Vultur* and *Gymnogyps*, the posterior ilia slope downward more rapidly and the borders of the ilio-ischiatic surface converge more noticeably than in *Breagyps*. In *Vultur*, the iliac crest recedes above the

TABLE 7
Measurements of Pelvis
(in millimeters)

	<i>Breagyps clarki</i> (3 specimens) ^a			<i>Gymnogyps californianus</i> (7 specimens)			<i>Vultur gryphus</i> (2 specimens)	
	max.	mean	min.	max.	mean	min.	max.	min.
Length synsacrum	146.4	143.6	141.5	152.3	142.0	134.5	163.0	139.6
Interacetabular width		55.8		57.0	53.8	49.8	61.2	55.8
Breadth across antitrochanters		82.4		83.0	79.8	74.6	92.8	85.8
Breadth across posterior iliac crests		79.1		85.9	82.9	80.7	84.1	77.9
Ratio (in %) interacetabular width to length synsacrum		39.2		40.6	38.0	33.8	42.5	37.5
Ratio (in %) breadth across posterior iliac crests to breadth across antitrochanters		96.3		108.1	103.9	102.1	90.8	90.6

^aOnly one pelvis measurable for dimensions other than length of synsacrum

acetabulum and the ilio-ischiatic fenestra; in *Gymnogyps* the crest is even more prominent than in *Breagyps*. The midline of the shield is narrower and more convex in *Gymnogyps* with greater depression laterally, but the perforations are similar to those of *Breagyps*; the reverse is true in *Vultur* (the midline is moderately convex as in *Breagyps*, but the perforations are fewer and smaller). In *Vultur* the point of greatest expansion of the synsacral caudal area (ventral view) is posterior to the acetabulum as in *Breagyps*, but a large pneumatic fenestra sets the synsacrum apart from the ventral surface of the ilia at this point; in *Gymnogyps* the expanded area is flush with the ventral surface of the posterior ilia as in *Breagyps*, but is farther forward.

Femur (Figure 8): Well flared proximal end, markedly protruding internally then narrowing abruptly in broad curve to slender shaft; shaft bowed anteriorly; trochanteric crest prominent, markedly deflected mediad and undercut by pneumatic foramina; obturator ridge sharply defined with deep depression adjacent internally below articular facet; attachment of round ligament (on head) deep and narrow; external intermuscular line forming sharp angle postero-externally at level of distal terminus of trochanteric crest. Distally, internal condyle protruding abruptly from shaft anteriorly; ligamental attach-

ment above fibular condyle large and facing proximally; rotular groove in line with shaft. See Table 8 for measurements.

The proximal flare is similar in *Vultur*, *Gymnogyps* is more columnar. However, in curvature of the shaft, *Gymnogyps* is more like *Breagyps*, *Vultur* is straighter. The trochanteric crest is less deflected in both the other condors although the arrangement of the foramina is similar in *Gymnogyps*; the obturator ridge is less sharply defined in *Vultur* and the adjacent depression shallower; in *Gymnogyps* the ridge is well defined but the depression tends to be narrower and deeper than in *Breagyps*. The attachment of the round ligament is broader but less deep, and the ligamental attachment above the fibular condyle is smaller and more posterior in position in both *Vultur* and *Gymnogyps*. The anterior contour of the internal condyle appears to be variable in *Gymnogyps*, so this may not be a valid character; it is, however, generally more abrupt than in *Vultur*. *Vultur* resembles *Breagyps* in placement of the rotular groove; the groove is more diagonally placed in *Gymnogyps* as a result of the mediad bending of the internal condyle.

Tibiotarsus (Figure 9): External cnemial crest longer than internal cnemial crest and having sharply compressed margin; internal crest (internal view) pinched in near proximal border; external proximal articular surface

TABLE 8
Measurements of Femur
(in millimeters)

	<i>Breagyps clarki</i> (9 bones)			<i>Gymnogyps californianus</i> (7 bones)			<i>Vultur gryphus</i> (2 bones)	
	max.	mean	min.	max.	mean	min.	max.	min.
Length from internal condyle to iliac facet	140.8	136.1	129.0	134.6	130.9	126.0	148.4	138.2
Greatest breadth proximal end	40.5	39.6	36.8	36.4	35.1	33.5	42.6	39.6
Greatest breadth distal end	39.0	37.5	35.3	36.2	34.8	33.7	39.5	38.1
Least dimension of shaft	16.5	15.5	14.5	16.8	15.7	15.0	16.7	15.7
Ratio (in %) breadth proximal end to length	30.1	29.2	28.2	27.0	26.8	26.3	28.7	28.6
Ratio (in %) breadth distal end to length	28.2	27.6	27.0	26.9	26.3	26.1	27.5	26.6
Ratio (in %) breadth of shaft to length	11.8	11.5	11.1	12.5	12.0	11.4	11.3	11.2

narrow and high. Distally, external condyle (anterior view) long and narrow with parallel sides and inclined so that proximal tip projects laterally, proximal contour of condyle blunt; ligamental attachment above external condyle well developed, somewhat triangular in shape with apex extending to level of upper edge of supratendinal bridge; lower margin of bridge tending to curl upwards resulting in large, unevenly shaped opening of tendinal canal. See Table 9 for measurements.

Vultur is similar to *Breagyps* in the character of the external crest, but the internal crest is more laterally deflected; distally, the external condyle in *Vultur* projects laterally but is broader; the ligamental attachment is smaller and the foramen more proximally placed. In *Gymnogyps* the external cnemial crest is shorter and less sharply compressed on the margin; the internal cnemial crest is less depressed near the proximal border; the external condyle is more vertically placed and tapers proximally; the ligamental attachment above the condyle is reduced. The proximal external articular surface is more broadly rounded and less raised in both *Vultur* and *Gymnogyps*, and distally the opening of the tendinal canal is more evenly oval.

Cervical vertebrae: The axis has been briefly described (Howard, 1969: 5-6) in connection with the discovery of a similar specimen in the Pleistocene deposits of Tequiquiac, Mexico. The characters distinguishing *Breagyps* from *Gymnogyps* and *Vultur* in this element are: the facets of the postzygapophyses are parallel, the posterior articulation of the centrum is broad and is directed posteriorly rather than dorsally, and the neural spine is broad and stubby. In both modern genera the facets of the postzygapophyses are aslant of the longitudinal axis of the vertebra, the posterior articulation of the centrum is narrower and faces more dorsally, and the neural spine is more slender.

The next *Breagyps* vertebra is either number 3 (immediately following the axis) or number 4. In this specimen, as in the axis, the facets of the post-

TABLE 9
Measurements of Tibiotarsus
(in millimeters)

	<i>Breagyps clarki</i> (4 bones)			<i>Gymnogyps californianus</i> ^a			<i>Vultur gryphus</i> (2 bones)	
	max.	mean	min.	max.	mean	min.	max.	min.
Greatest length	233 ^{est}	223	214	213	210	208	251	236
Length to proximal articulation	225 ^{est}	216	209				244	230
Breadth distal end	25.7	24.4	23.7	25.5	24.3	23.3	26.2	25.4

^aMeasurements as given by Fisher (1947:234). Length assumed to be greatest length but not so stated. Single available LACM specimen measures 218 mm greatest length, 213 mm to proximal articulation, breadth distal end 23.5 mm.

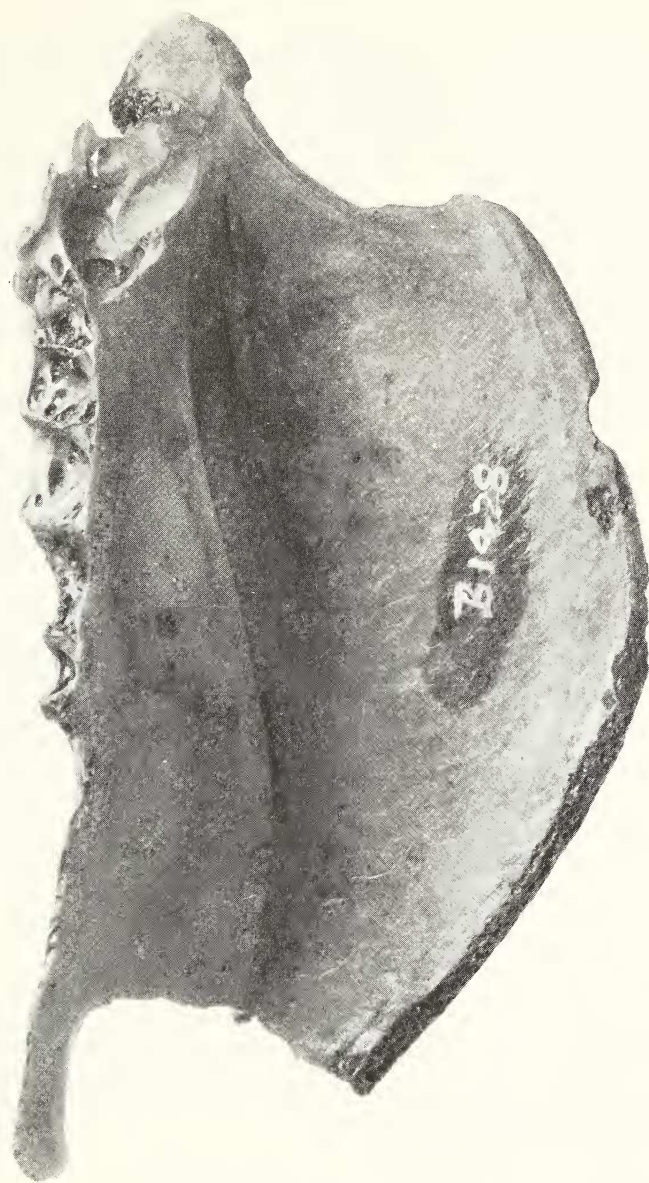


FIGURE 1. *Breagyps clarki*, sternum, B1428 (now in mounted skeleton on display).
X 1.

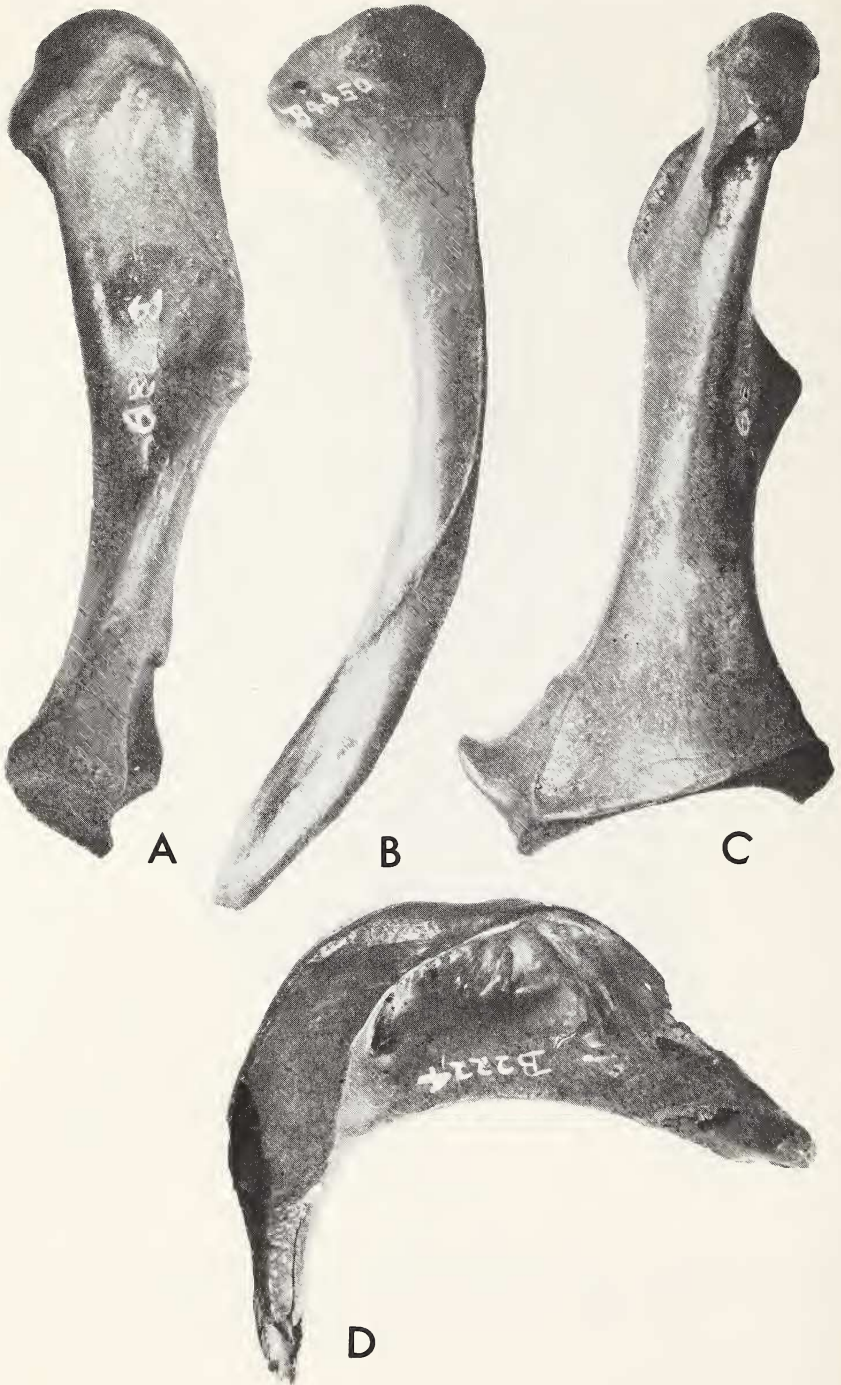


FIGURE 2. *Breagyps clarki*. A. internal, and C. anterior views of right coracoid, B1739; B. right scapula, B4450, ventral view; D. left clavicle, B2224, external view. X 1.

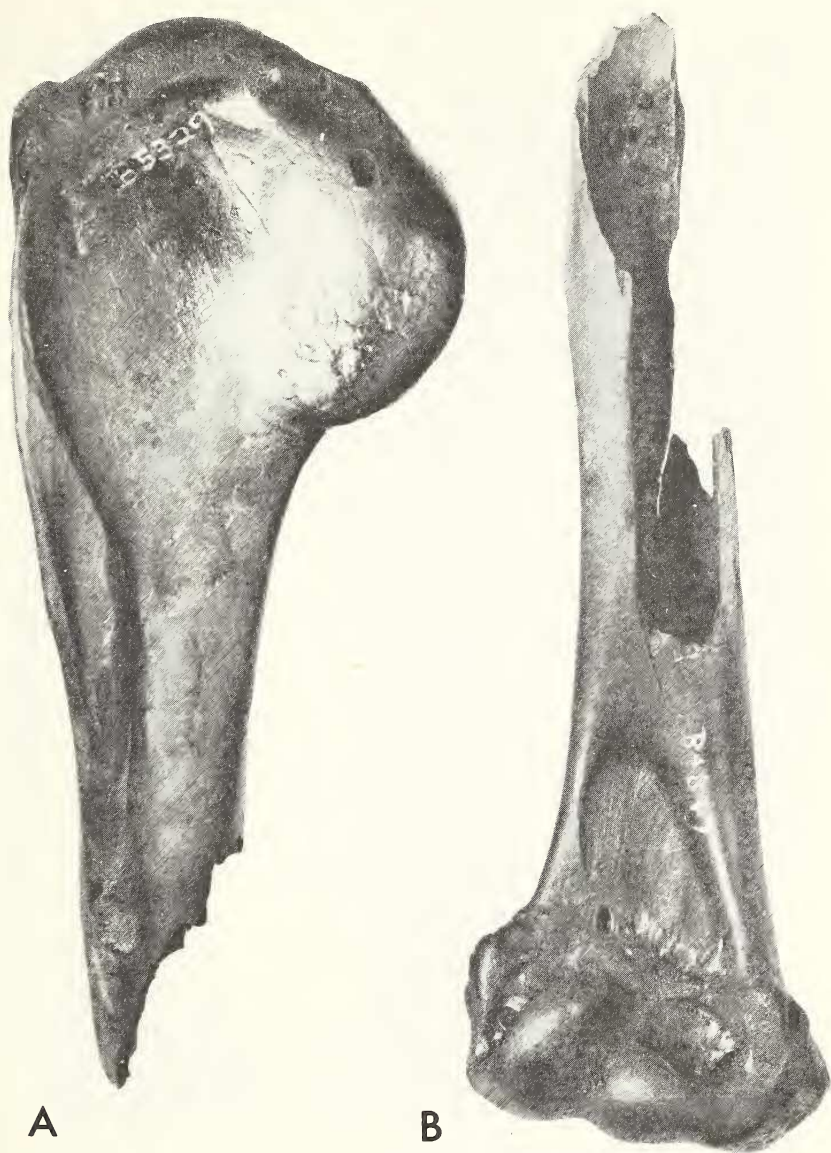


FIGURE 3. *Breagyps clarki*, right humerus. A. proximal (B5329), and B. distal (B4847) ends of same bone, palmar view. X 1.

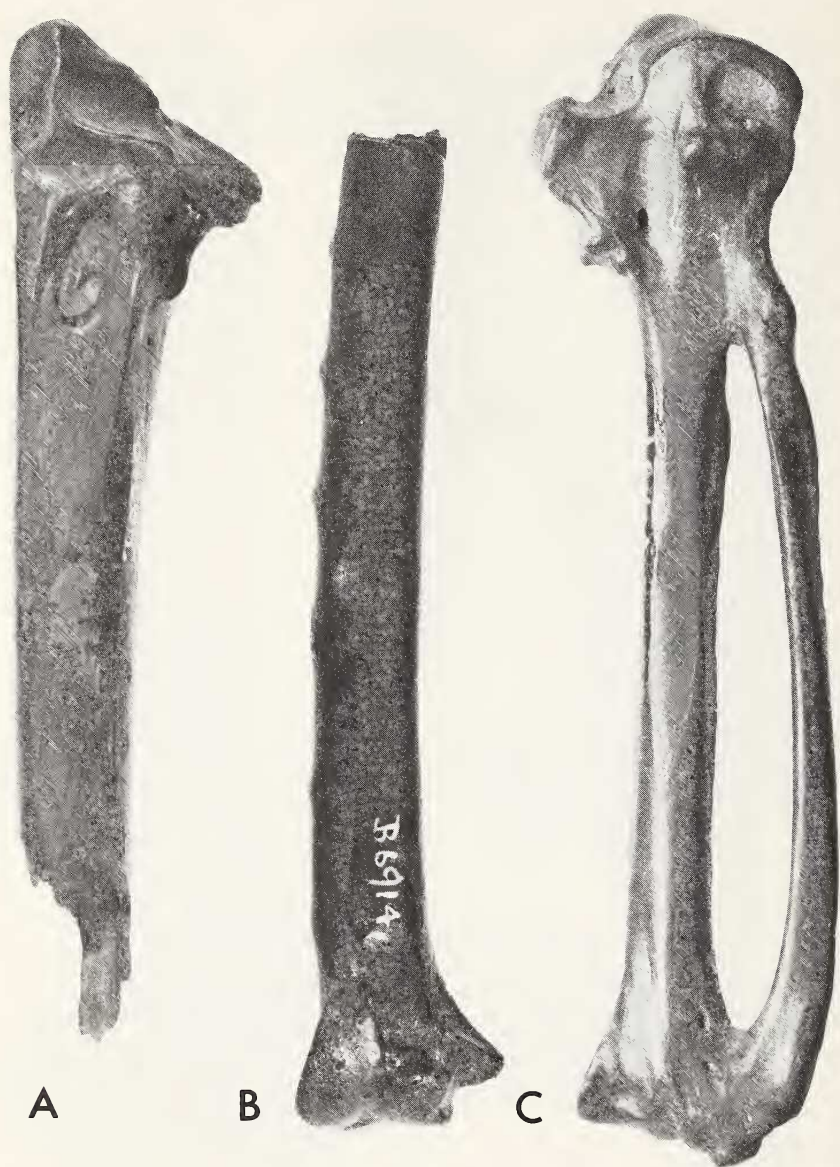


FIGURE 4. *Breagyps clarki*. A. proximal end of left ulna, B8310, internal view; B. distal end of left ulna, B6914, internal view; C. right carpometacarpus, J9402, internal view (previously figured (Miller, 1925) as *Cathartornis gracilis* and later (Miller and Howard, 1938) assigned to *B. clarki*).



FIGURE 5. *Breagyps clarki*. A. proximal end of right radius, B6782, external view; B. proximal end of right humerus, B5329, anconal view; C. distal end of right radius, B7661, palmar view. X 1.

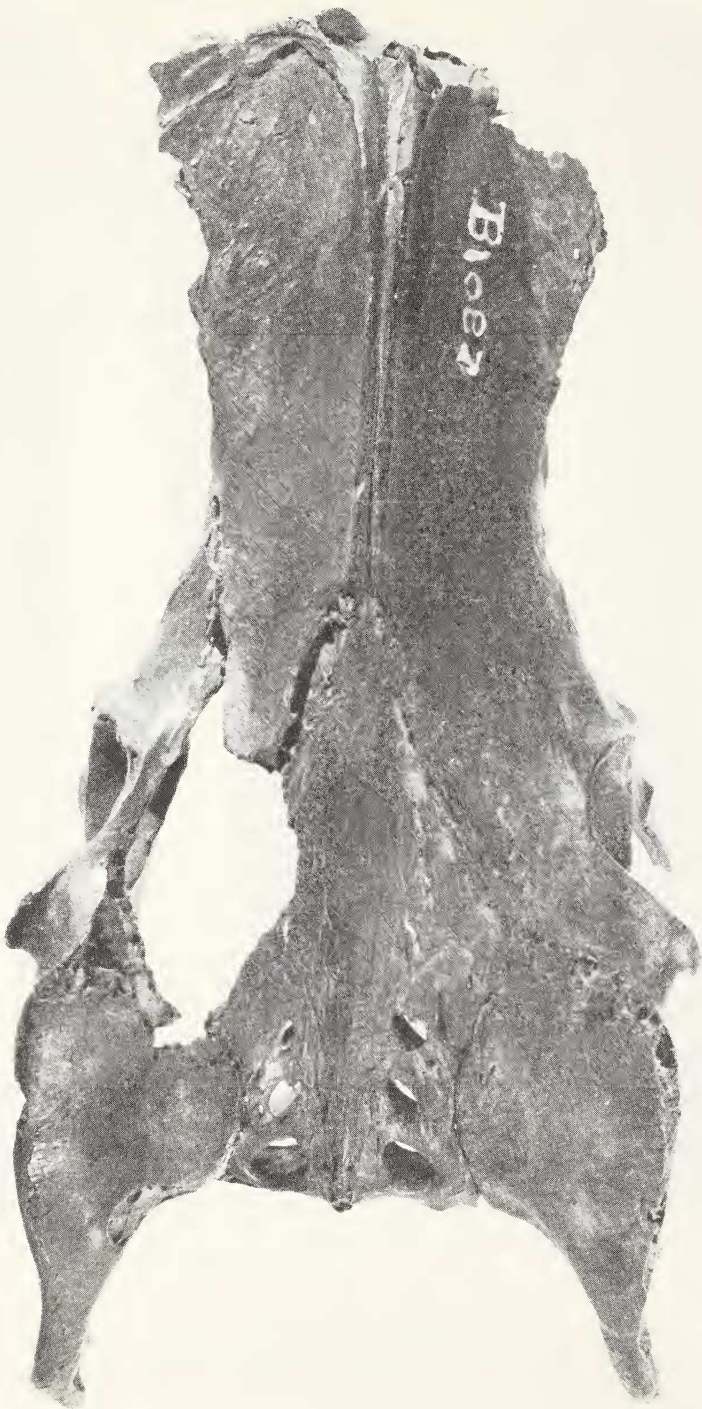


FIGURE 6. *Breagyps clarki*, pelvis, B1082+B1092, dorsal view. Approx. X 1.



FIGURE 7. *Breagyps clarki*, pelvis, B1082+B1092, lateral view. Approx. X 1.



FIGURE 8. *Breagyps clarki*, left femur, B5580. A. anterior view; B. external view. X 1.

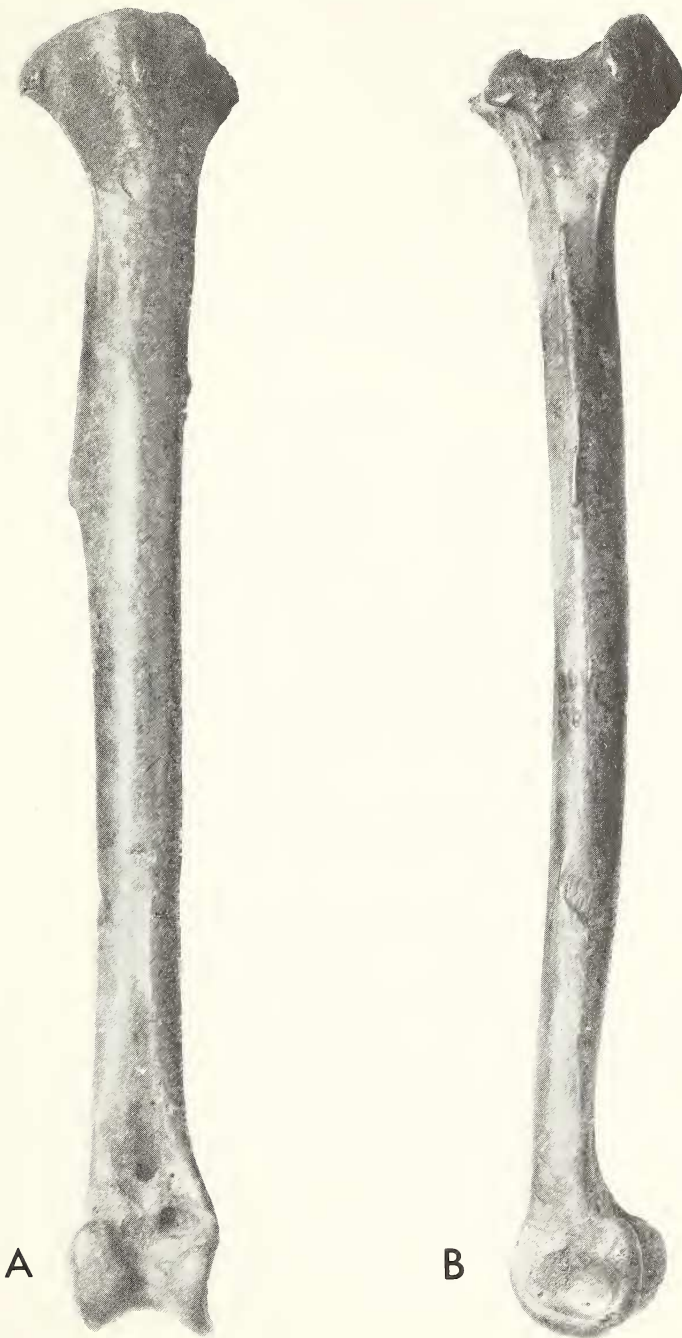


FIGURE 9. *Breagyps clarki*, right tibiotarsus, B5878. A. anterior view; B. external view. Approx. $\times \frac{3}{4}$.

zygapophyses are parallel in position and the posterior articulation of the centrum faces more posteriorly than dorsally. Also, as in the axis, the neural spine is broad and stubby. These characters distinguish the *Breagyps* vertebra from the cervicals of either modern condor genus.

The other two vertebrae resemble cervical number 6 of *Gymnogyps* in the deep V-shaped posterior contour which separates the postzygapophyses, but they differ from this element in *Gymnogyps* in that the facets of the prezygapophyses face more anteriorly. In this respect they more closely resemble cervical number 5 of *Vultur*, though the posterior contour in this latter is less acutely V-shaped. The neural spine on the fossil specimens is more nearly centered (in antero-posterior direction) than in the specimens of either of the other condors. In these latter, the spine is more anteriorly placed.

DISCUSSION

As previously noted, *Breagyps* shares some separate characters with other cathartid genera but may be clearly differentiated by the combinations of its characteristics. The foregoing section has demonstrated these points with respect to comparison with *Vultur* and *Gymnogyps*. There appear to be more areas of similarity with the former. In summary, the most notable points of resemblance to *Vultur* are found in the general shape of the sternum, humerus, radius and femur and in the details of the cnemial crests of the tibiotarsus. But even in these elements, detailed differences exist. The most notable distinctions, however, are found in the furcula, scapula, ulna and carpometacarpus.

Although marked differences from *Gymnogyps* occur in all elements, resemblance is noted in a few detailed characters: triangular depression on ventral labial prominences of sternum, deep pneumatic fossa undercutting dorsal rim of furcula, rounded dorsal contour of acromion of scapula, degree of pneumaticity of distal end of humerus, curvature of femoral shaft and projecting posterior iliac crests of pelvis.

Areas of resemblance to the smaller vultures are given below.

The sternum of *Coragyps* resembles that of *Breagyps* in the broad, straight anterior contour and the shape of the carina. In *Coragyps*, however, the point at which the carina ascends is more posterior, the dorsal area of the shield less depressed, the ventral labial prominences lack the triangular depression, and the ventral manubrial spine is more prominent. The coracoid of *Coragyps* resembles that of *Breagyps* in the protruding brachial tuberosity and angular border of the fossa beneath, but the furcular facet is narrower, the ligamental attachment on the external side of the head less prominent and the neck less depressed. In the pelvis, *Coragyps* resembles *Breagyps* in the depth of the ilioischiatric area, the prominence of the posterior iliac crests and the condition of the synsacral caudal area. The shield, however, is set lower with respect to the ilia and is flatter and more perforated; also there are only two synsacral thoracic vertebrae.

The ulnae of both *Coragyps* and *Sarcoramphus* have the area between the

brachial impression and the internal cotyla swollen as in *Breagyps*, but the area is much more pneumatic in *Coragyps*, and, in *Sarcoramphus*, the brachial impression is more deeply depressed adjacent to the heavy, abruptly flared anconal border. Furthermore, in both *Coragyps* and *Sarcoramphus*, the internal contour of the proximal end from olecranon to cotyla is more nearly straight, the olecranon less clearly defined than in *Breagyps*. Also, these smaller vultures have fewer anconal papillae for the secondaries and, distally, both have a longer, narrower external condyle.

In *Sarcoramphus* the bicipital crest of the humerus is rounded as in *Breagyps* and the distal tip of the pectoral attachment is laterally placed. Other characters of the humerus described for *Breagyps* are, however, different in *Sarcoramphus*. The femur of *Sarcoramphus* resembles that of *Breagyps* in the mediad deflection of the trochanteric crest and in the anterior contour of the internal condyle, but is otherwise distinct.

Even *Cathartes*, which is least like *Breagyps* throughout the skeleton, shares one character of the humerus not found in any of the other genera, namely the bordering rim and mediad depression of the deltoid crest. The contour of the crest, however, is more flared and angular.

Distinctive detailed characters of *Breagyps*, not found in any of the other genera, are:

Sternum: Dorsal area of shield more deeply depressed back of heavy anterior swelling; apex of carina at level of last costal process.

Furcula: Deep pneumatic fossa undercutting dorsal rim of clavicle but ending above its ventral border; abrupt expansion back of pointed scapular tip with foramen above.

Scapula: Short, abruptly flared acromion with marked mediad deflection dorsally.

Coracoid: Uneven contour of head with marked diagonal groove through furcular facet.

Ulna: Short, heavy external condyle.

Radius: Abruptly flared distal end.

Carpometacarpus: High, more upturned process of metacarpal 1; marked depression of proximal symphysis and short, prominent tuberosity of metacarpal 2.

Femur: Large ligamental attachment above fibular condyle facing proximally, and deep, narrow attachment of round ligament.

Tibiotarsus: Blunt external condyle projecting laterally.

With respect to size, *Breagyps clarki* averages generally larger than *Gymnogyps californianus* and is notably broader and deeper chested. Greater wing length is gained through the distal segments; the four complete fossil humeri are all shorter than the four available of *G. californianus*. Although ulnar length can only be estimated for *Breagyps clarki*, the very smallest estimate exceeds the maximum for *G. californianus* by 18 mm. The carpo-

metacarpi average 5 mm greater than the larger of the two available *G. californianus* specimens.

The larger of the two comparative skeletons of *Vultur gryphus* exceeds *Breagyps clarki* in nearly all measurements. The smaller skeleton, however, falls within the range of the fossil bones in many areas. In general, compared to this minimum *Vultur* specimen, the fossil species averages slightly narrower, though deeper through the chest, the wings slightly longer and differently proportioned, the legs shorter in all elements though proportionately longer in the femora. (See tables).

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